INHERITANCE OF SOME BODY CHARACTERS IN DAIRY CATTLE

by

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INTRODUCTION

Little is known of the mode of inheritance of the component parts of dairy cattle. This is partially due to the difficulties usually encountered in working with large animals, such as: length of generation, expense in carrying on controlled experiments in which the uneconomical as well as the economical individuals are kept, scarcity of parent-progeny comparisons except by records or photographs, lack of authenticity of long time records, and the personal equation in obtaining measurements or estimations. In spite of these limitations an abundance of material is available in the thousands of purebred and grade dairy cattle born each year in the United States, if only enough interest were shown by the breeders and animal geneticists to record, analyse, and make a genetic interpretation of the characters involved.

For more than 80 years most of the dairy breeds have been represented by official score cards on which the ideal body parts have been described. Serious thought has been given to these descriptive standards, and occasionally, when "improvement" seemed needed they have been changed. Several million cattle of the combined five major dairy cattle breeds have been bred and registered in the herd books of the respective associations since the breed score cards were adopted as ideals toward which to strive.

Genetic analysis of inheritance has been attempted on only a few of the more easily compared characters, such as coat color, lethals, and conformational anomalies. The inheritance of production has been the subject of much research primarily because of its economic value, while very little attention has been given to the inheritance of conformation and size.

If linkage could be determined between the inheritance of some body parts and milk or butterfat production, the interest in the inheritance of these characters would be strengthened. There is a need for such study for if any relationship does exist between a body character and production, it cannot be determined until the mode of inheritance of the body character has been decided; also, regardless of production, if animal husbandmen are striving to breed toward an ideal (and most breeders of all types of livestock are) they need to know how to mate animals to accomplish their purpose.

There are many gross parts of an animal, all of which the breeder must attempt to perfect at the same time in his breeding operations. Some are apparently of more economic importance, and some are more easily measured than others. With so little known, the study of their inheritance can justifiably be done in the order of their feasibility, the value to the breeder increasing as the knowledge accumulates.

As evidence of the need for this study, a list of suggested heritable characters has been presented (Table 9, Appendix). In this list are some characters which have never before been reported in the literature, others are recognized commonly by the breeders as faults, but all are found occurring too frequently to question their heritability. Shape of udder, veining, and others of the more obvious characters have purposely been omitted.

Since skeletal conformation and abnormalities are among the more easily measured characteristics of cattle and are less influenced by environmental conditions than are capacity, mammary system, or producing ability, most of the emphasis in this study was placed on measurements of this type.

REVIEW OF LITERATURE

In this paper no attempt has been made to review the literature on the inheritance of milk production. Attention has been confined to physical characters, with the greatest emphasis on those of conformation, size, and body parts.

Inheritance of Coat Color

Coat color has been the subject of more genetic analysis than any other characteristic, not because of its economic value, but because of the ease of observation. Ibsen (1933) presented a complete survey of the subject from his own observations and from material obtained from other publications on color inheritance (Table 10, Appendix). He stated that there are only two pigments found in cattle, black represented by B, and red represented by R, these pigments being found in all animals, but being influenced in expression and pattern by 17 different modifiers. Bogart and Ibsen (1937) studied more specifically the phenogenetics of color in cattle and confirmed most of Ibsen's (1933) previous theories.

Inheritance of Lethals

The term "lethals" is used in genetics as meaning any inherited factor which results in the death of the individual either before or after birth. Several lethal characters in dairy cattle have been quite fully described and modes of inheritance established.

Hutt (1934) listed 11 lethal factors in dairy cattle, and Eaton (1937) gave a more complete list of 14 characters including two types of achondroplasia, amputated legs, ossification or articulation of lower jaw, congenital

dropsy, congenital ichthyosis, epithelial imperfections, foetal resorption, hairlessness, impacted molars, muscle contracture, mummification, short limbs, and short spine. In a Jersey herd Ely, Hull, and Morrison (1939) found another lethal factor, agnathia, or absence of the lower jaw. They reported this to be a male limited, recessive factor. Shaw (1938) found two full sisters in a Holstein herd, each with a hole in the front of the skull; this condition he called meningoencephalocele and proencephalus of cranioschisis. No genetic explanation was offered.

A complete list of lethal characters is given in Table 12, Appendix.

Inheritance of Conformation

Much attention has been paid to the conformation, form, and type of dairy cattle, and the similarity or dissimilarity of appearance has often been noted among the daughters of one sire. The genetic mode of inheritance of these characteristics, however, has not been determined.

Pontius (1922), Reimers (1925), and others have noted a general relationship between linear measurements of various body parts, not only in dairy cattle but for animals in general. These relationships have then been put into practice as an "infallible rule"[1] in judging the proportions of animals, the length of head having been taken as the yardstick to equal, for instance, the width through shoulder points, length of thigh, etc. While this opinion may be applicable in general observation, it would not be strictly true when comparing measurements.

A formula for estimating the surface area from body weight has been proposed by Elting (1926). In a study of the accuracy of body weights, Lush,

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[1] Letter from Mr. Ross Butler to Professor F. W. Atkeson, November 9, 1938.

Christenson, Wilson, and Black (1928) found under normal conditions that the standard deviation on single weights was between six and 12 pounds, and that averages of thee-day weights eliminated about 42 percent of this error. Davis, Morgan, Brody, and Ragsdale (1937) prepared a table to determine the weight of dairy cattle from height or from chest girth. Basing their conclusions on 10,921 pairs of weights and measurements they arrived at the following formulas:

$$\text{Weight} = 0.000041 \times \text{height}^{4.38}$$

$$\text{Weight} = 0.0058 \times \text{chest girth}^{2.88}$$

Lush and Copeland (1930) studied the accuracy of dairy cattle measurements by measuring nine Jersey cows 11 times each. Of the 28 measurements they found that dewlap area had the largest standard deviation, 17.2 percent of the average of all nine cows, and length of head had the smallest, 0.49 percent. Cannon circumference, width at hips, height over withers, and heart girth were the next most accurate measurements.

These and other studies, Eckles and Swett (1918), Eckles (1920), Brody and Ragsdale (1924), Swett, Graves, and Miller (1928), Graves and Miller (1932), Swett and Graves (1939), have been valuable in determining average growth curves, average size of parts, and average linear measurements. These experiments have also been of value in outlining procedures to follow in taking measurements as well as indicating sources of variation. In the same category are several other experiments a little more closely connected with mode of inheritance: Gowen (1920a, 1921, 1923), Anthony (1930), Swett, Miller, Graves, and Creech (1932), Miller, Graves, Black, and Creech (1937), Davis and Willett (1938), and Cristen (1935), in which the relationships between certain body characters and milk production have been studied.

Inheritance of Size

As early as 1914 MacDowell and Castle (1914) demonstrated inheritance of size in rabbits. Since they found a high correlation between various skeletal measurements on the same animal, they stated that the factors which affect skeletal size are to a large extent general factors affecting all parts the same. Ritzman (1923), although not contradicting MacDowell and Castle (1914), showed that in sheep, the size of structural units may be controlled by factors which are inherited independently. Castle (1929) had found differences in two races of rabbits and their crossbred progeny, but since he was unable to demonstrate any linkage between size genes and the color genes agouti, black, intense, and English, he postulated that size might be controlled by factors other than genes. However, in a mouse species cross (Mus musculus X Mus bactrianus) Green (1931b) stated that he had "indubitably shown an association in heredity between factors productive of a large size in several quantitative characters and a recessive qualitative character, brown coat color". This result rather firmly established the fact that at least in mice, general size is influenced by chromosomal genes, not by some extra-chromosomal material as suggested by Castle (1932). The discussion of whether size factors were predominantly general or specific in nature was quite sharp between Castle (1932) and Green (1932), with such men as Wright (1932) adopting a neutral stand in which both types were considered important. A general difference in growth rate was indicated in work done by Gregory and Castle (1931) on the embryological basis of size inheritance in rabbits. By statistical analysis they found significantly higher numbers of blastomeres in the large race rabbits than in the small race as early as 41 hours, about the time the eight-cell stage was just passing into the 16-cell stage.

In a study of human stature, Davenport (1917) concluded that due to the variability found in matings of short X short and the uniformity of tall or very tall X tall or very tall that there are at least two dominant growth inhibiting factors. He also sated that proportional inheritance was just as evident as absolute inheritance.

A conformational index to be used in cattle was proposed and tested by Gregory (1933) in which horizontal round measurement from patella to patella was divided by the height at the withers. Using correlation coefficients he indicated that the genetic factors controlling muscle diameter are different in nature if not independent of linear measurements. The index was constant from birth in beef cattle and increased from birth to eight months in dairy cattle, indicating that the differences in birth weight of the two types of cattle was due more to differences in muscular development than to any other one factor.

Inheritance of Miscellaneous Characters

Among the more easily detected and analyzed characters of dairy cattle are the conformational anomalies, or deviations from the normal appearance. The inheritance of anomalies has attracted much investigation, for although variable, a distinction can usually be made between the animals affected and those not. This is in direct contrast to such characters as size and conformation in which all gradations between the extremes may be found.

A case of polydactylism in cattle in which the affected animals had three or more toes on each foot was reported as a dominant in a grade Holstein by Roberts (1921). Lush (1930) reported a condition of short legs in some Texas cattle, known as "duck-legged," which was inherited as a dominant. This condition appeared similar to one Eaton (1937) reported Wilson to have found in Irish Dexter cattle, except that there was no association with the lethal

character of "bull-dog" calves.

Lush (1922) reported a case of notched ears in Jersey cattle that was dominant. Lush (1924) also found a case of double ears in some crossbred Brahma cattle, a condition in which a fin-like projection of cartilage extended from the back of the ear. It exhibited all the qualifications of a dominant character in the observations that were made.

Atkeson and Warren (1935) determined that wry tail in Jerseys is a recessive character. In a herd of inbred Red Polled cattle Knapp, Emmel, and Ward (1936) reported a condition known as kinky or screw tail. This anomaly, which is also a recessive, is similar to wry tail except that it affects the tail nearer the tip than the base, giving the appearance of a broken tail. Modifying factors determine the number of vertebrae affected. Another condition very similar to wry tail but inherited as a dominant character was described by Roemmele (1935) in a Brown Allgau cow and offspring. In this case the sacral vertebrae were developed more on one side than the other, with the intervertebral discs of unequal size and shifted to the side.

Auld (1927) reported that the polled or hornless condition of cattle has been known for centuries, some of the early Roman coins having pictures of polled bulls. He also stated that polled animals represent the most primitive form of cattle known, horned individuals coming later from polled ones. Polled is a dominant factor, but has many modifications not yet completely understood.

Detlefsen and Yapp (1920) reported a recessive condition of congenital cataract. Heizer (1932) found an udder abnormality behaving as a recessive in purebred Guernseys in which the one side of the udder had only one teat. Semi-hairlessness, a condition approaching the lethal condition of congenital ichthyosis, was discovered to be recessive in some Polled Herefords by Craft

and Blizzard (1934). Warren and Atkeson (1931) indicated that hernia in a family of Holsteins was a sex limited dominant factor.

Among the characters reported to be inherited, but the mode of which is not yet known, are defective hair and teeth reported by Cole (1919), twinning in a Holstein family by Lush (1925), double muscled condition known for many years, but mentioned again by Weber and Ibsen (1934), and tongue rolling reported by Weber (1939).

As early as 1910 Carlo Pucci stated that the Zebu skeleton, dewlap, ear, and musculature were dominant to the Italian cattle, while skin color and horn size were recessive (crosses with zebu cattle, 1916). In the Jersey X Angus cross Gowen (1918) stated that beef quality in the forequarters and dairy quality in the rear quarters were dominant. Also Gowen (1920a) stated that high milk yield and low fat percentage appeared to be dominant. However, it must be borne in mind that these characters are observational and subject to personal opinion, not definitely proved Mendelian dominance.

MATERIALS AND METHODS

The materials or subjects used for most of this study were cows two years old and over in the Kansas state institutional dairy herds. Since controlled, experimental mating of these cattle for specific genetic characters has not been practiced, and since only one year was available for this study, the characters were analyzed by collecting as much information as was available on groups of five or more daughters of individual bulls. Wherever possible, measurements were made of the sires and of the dams, but only eight out of 22 sires were available, and six was the largest number of dam-daughter pairs within a group of daughters of one bull. Since such a limited number of dams was available for measurement, only the data from the daughters could be treated statistically.

The methods employed for obtaining the data will be discussed at the beginning of each section under presentation of experimental data.

PRESENTATION OF EXPERIMENTAL DATA

Head Measurements

Variations of Head Measurements Within the Holstein Breed. Length and width of head were measured on 248 Holstein cows two years old or over which were daughters of 19 different bulls located in six different herds. Head length, the overall measurement from poll to nose, was determined with a sliding rod on a brass Dietzgen meter stick (Fig. 7B, Appendix). The width was measured by placing the same meter stick horizontally across the cow's head and moving it from the poll toward the nose, simultaneously adjusting the sliding rod until it slipped over the widest point. Duplicate measurements never varied more than 1 cm, or approximately five percent of the width and three percent of the length. Since the measurements were only read to 0.5 cm, duplicate measurements were considered unnecessary.

By the following analysis it has been shown that within one breed the measurements of head width and head length are more constant within a group of daughters of one bull than they are between groups of daughters of different bulls.

Since length and width of head had a highly significant correlation of 0.437, coefficients of variation (Snedecor, 1940 p. 40) were calculated to determine whether dividing length by width would provide a more constant value than either measurement separately. The coefficients of variation, however, were nearly the same; 4.15 percent for length, 5.88 percent for width, and 4.18 percent for the ratio of length divided by width. Since no reduction in

comparative variability was obtained, an analysis of variance was made separately on each measurement as well as on the ratio.

Age of the animal plotted against head length, width, and the ratio of length divided by width gave a slight positive regression as indicated by scatter diagrams. A correlation coefficient (r) of 0.409 was obtained from the most favorable comparison, age and head width. Although this correlation was highly significant, it revealed that only 17 percent* of the variation within this group of cows was caused by differences in age. It was evident, therefore, that in head measurements of cows over two years old, age is of secondary importance, and some other source or sources caused the greatest amount of variation.

These animals were then divided into 19 groups according to sires (Table 1), and by an analysis of variance (Snedecor 1940 p. 179) the relative variation between these groups was tested to determine if this variation was greater than could occur by sampling error. A very highly significant F value was obtained in the analysis of head length 10.67, and of head ratio 9.19, indicating that the probability was at least 1000 : 1 that the groups of daughters differed in these values more than could be accounted for by random variation. The F value in the analysis of variance of head width was 3.13, which, although highly significant, was much smaller than the F values of head length and head ratio.

From this study it has been shown that within one breed the measurements of head width and head length are more constant within a group of daughters of one bull than they are between groups of daughters of different bulls. Since the F value for width, however, was much smaller than the F value for length, it appeared that width is probably controlled for the most part by factors which determine the general size of the animal, while length is closely

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*Snedecor, 1940. p. 138. "—r^2 (correlation coefficient)^2 is the fraction of Sy^2(sum of the squares of the deviations from the mean) associated with correlated changes in X and Y (the two variables, in this case head width and age)—".

associated with special size factors specifically increasing or decreasing head length without causing a proportional change in head width.

Table 1. Head measurements of 246 Holstein cows grouped according to sires.

Bull	No. of daughters	Avg. length	Standard deviation	Avg. width	Standard deviation	Avg. ratio	Standard deviation
1	24	54.9	1.44	23.7	0.77	2.32	.051
2	8	52.9	1.27	22.7	0.70	2.33	.046
3	13	55.5	1.41	23.0	0.72	2.41	.104
4	12	55.6	1.51	23.6	0.93	2.36	.097
5	7	54.6	0.93	23.6	1.07	2.31	.103
6	17	51.6	1.85	22.5	0.81	2.27	.091
7	6	55.6	1.20	23.5	0.76	2.29	.057
8	7	52.1	1.22	22.4	0.35	2.32	.063
9	9	55.1	2.01	23.2	1.09	2.29	.067
10	9	52.0	1.73	23.9	0.60	2.18	.066
11	8	49.5	1.51	23.0	0.43	2.15	.050
12	25	51.8	1.56	23.1	0.72	2.24	.061
13	30	51.9	2.30	23.4	0.86	2.22	.082
14	28	53.6	1.57	22.9	0.59	2.34	.076
15	5	53.4	1.95	23.6	0.96	2.26	.078
16	6	52.7	1.55	22.2	1.17	2.38	.061
17	10	52.8	1.60	23.1	0.74	2.29	.085
18	5	52.5	1.92	23.1	0.96	2.29	.098
19	17	54.6	1.76	23.4	0.82	2.34	.074

The average head length measurements of each bull's daughters, when plotted in order of increasing length (Plate III, Fig. 2, Appendix) showed a definite grouping. Eight daughters of one bull formed the group with the shortest heads, 72 daughters of five bulls formed the group with the longest heads, and the remaining 166 daughters of 13 bulls formed an intermediate group. In order to determine if this grouping could be caused by a short head factor incompletely dominant to long head, the frequency distribution in Fig. 1 was plotted. Although dominance of one character or the other could not be demonstrated, it appeared that the intermediate group showed more heterozygosity than either of

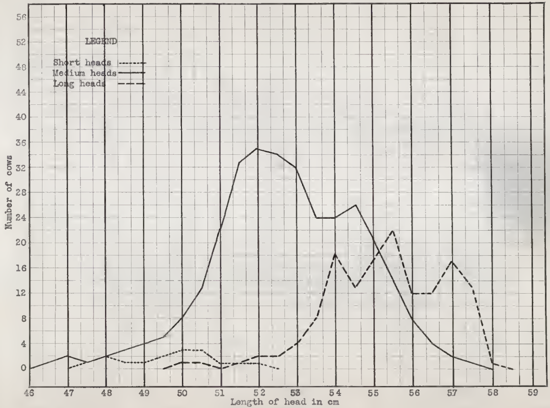


Fig. 1 Frequency distribution for length of head. Points determined by a two-place moving average.

the extreme groups. This would not necessarily indicate a single factor, but a single factor would be the simplest explanation fitting the available data.

Additional evidence that head length is inherited by Mendelian factors was obtained by comparing the head lengths of the available dams with their daughters (Table 2). The average head lengths of the daughters of sire No. 2 was 52.9 cm, yet when this bull was bred to a dam measuring 57.0 cm a daughter was produced with a head length of 52.0 cm. Therefore the dam, although

Table 2. Comparison of dams to daughters in length of head.

Sire No. 1 avg. 54.9		Sire No. 2 avg. 52.9		Sire No. 4 avg. 55.8		Sire No. 11 avg. 49.5	
Dam	Daughter	Dam	Daughter	Dam	Daughter	Dam	Daughter
56.5	54.0	55.0	54.0	56.0	57.0	53.0	47.5
53.5	55.0	57.0	52.0	56.0	55.0	52.0	48.5
53.5	55.0	55.0	55.0	57.0	54.0	51.5	50.0
56.5	54.0						
55.5	56.0						
52.5	51.5						

carrying the factor for long head, apparently transmitted some characters for short head. Another dam, with a head length of 55.0 cm, when bred to the same bull, produced a daughter measuring 55.0 cm, indicating that the short head of the first case was not necessarily a result of the bull's prepotency.

From the foregoing data obtained from measuring 248 Holstein cows, daughters of 19 different bulls, it has been shown that length and width of head are determined by inheritance. Both measurements are probably controlled by general size factors, but length appears to be also influenced by at least one pair of special size factors.

Variations in Head Measurements Between Breeds. In the Kansas State College herd the length and width of the heads of 69 cows of four different breeds (22 Holstein, 16 Ayrshire, 12 Jersey, and 18 Guernsey) were measured. The Holsteins were daughters of seven different bulls, the Ayrshires of five different bulls, the Jerseys of four different bulls and Guernseys of eight different bulls. Representative samples of the breeds were thus formed without any undue influence of one sire. Additional evidence that these samples were representative was shown by the close similarity between the head ratio of the Holsteins in this herd and that of the 248 cows in the other herds, 2.296 and 2.292, respectively.

Comparison of the four breeds for head measurement, by analysis of variance, showed a very highly significant F value; and by a subsequent t-test the animals were classified into three groups, Holsteins having the longest heads, the Guernseys and Ayrshires have the medium sized heads, and the Jerseys having the shortest heads. Head length, by analysis of variance, was found to have a very highly significant F value of 48.92, while head width, as in the previous Holstein study, had a much smaller F value of 4.06, just approaching the highly significant level. From this it was concluded that width varied as significantly between families within the Holstein breed as it did between breeds. Length, however, as shown in Table 3, varied much more between breeds than it did between families in the Holstein breed. The variation in head width between the Jerseys and Holsteins (Table 3) was only 0.45 cm, or 1.95 percent, using the Holstein average as the base. Head length, however, showed a noticeable differency of 8.76 cm, or 16.65 percent.

Table 3. Head measurements of 69 cows of four different breeds.

Breed	No. of animals	Avg. length	Standard deviation	Avg. width	Standard deviation	Avg. ratio	Standard deviation
Holstein	22	52.68	2.36	22.95	1.08	2.296	.070
Ayrshire	16	48.72	2.76	22.25	1.29	2.191	.082
Guernsey	18	47.08	1.51	21.80	0.82	2.165	.088
Jersey	12	43.92	1.58	22.50	0.98	1.953	.082

Since early in this study it was indicated that highly significant differences in head length existed between breeds, a test was conducted to determine whether this was due to differences in overall length or to one portion of the head length only. The length from eye level to nose therefore was measured on the 69 cows of the college herd. Total length of head was then divided by this measurement of eye level to nose to obtain a ratio proportional to the total size of the head. In Holsteins this ratio was found to be 1.86 - .04, in Ayrshires 1.85 - .06, in Jerseys 1.86 - .05, and in Guernseys 1.86 - .05. It was concluded, therefore, that although a very highly significant difference exists between breeds in total length of head, the proportion that they eye level to nose is of the total head length remains constant.

Body Depth

Some cattle are criticized by breeders as being "leggy," referring to the fact that their body is not deep enough in proportion to the total height of the animal. Depth percentage (depth divided by total height X 100) was chosen as a single value to represent this condition. The height just behind the withers and the depth of body just behind the shoulder points were the measurements that were made in six herds, on 250 cows, daughters of 17 different bulls being represented.

These measurements were made with a brass Dietzgen measuring rod (Fig. 7A, Appendix). The animals were all measured on concrete floors while standing in milking stanchions. The upright rod was placed beside the animal so that the lower arm or bar was underneath and directly behind the front legs. The upper arm was placed directly above the lower arm and over the cow. The lower arm was raised until it pressed firmly against the floor of the chest and the upper arm lowered until it rested on the cow's back. The vertical position of the upright rod was then established by the use of a spirit level located in the upper arm. The position of the lower arm was then checked and the entire rod removed and read. Duplicate measurements were not taken.

The animals varied widely in the three values, height, body depth, and depth percentage. The range was for total height 125 to 147 cm, for body depth 65 to 86 cm, and for depth percentage 51.8 to 60.7 percent. It was found, however, that the variation was greater between groups of daughters of different sires than between daughters within a group of one sire. From these results it was therefore concluded that these differences must be due to inheritance.

Scatter diagrams were made plotting the age of the animal against the height, the body depth and depth percentage. Although a very highly significant correlation of 0.384 was found between depth percentage and age, it only represented 15 percent of the total variation, therefore age was not considered in the analysis of variance of any of the characters.

These animals were divided according to sires into 17 groups (Table 4) to be treated by an analysis of variance. The F values obtained were 4.36 for height, 3.96 for depth, and 3.29 for depth percentage. These very highly significant values were strong evidence in favor of the inheritance of these characters. Supporting evidence for the assumption that legginess is inherited

was the wide difference existing between the average depth percentage of the daughters of the four bulls No. 11, 14, 8, and 13, and the daughters of the two bulls No. 15 and four (Plate III, Fig. 1, Appendix, and Table 4). A striking difference was also noted between the daughters of bull No. 11 and bull No. 1 in height (Plate III, Fig. 3, Appendix, and Table 4).

No factorial analysis was attempted since a significant break could not be demonstrated in the array of averages of the bulls' daughter (Plate III, Fig. 1, Appendix). Since the F values were very similar, no special factors that affected either total height or body depth without affecting the other measurement could be postulated.

Table 4. Body measurements of 230 Holstein cows grouped according to sires.

Bull	Bull's measurements H*	D**	D%#	No. of daughters	Avg. D	s##	Avg. H	s	Avg. D%	s
18	142	61	57.0	5	133.2	3.26	72.2	3.12	54.18	1.32
14	——	——	——	28	137.4	2.78	74.6	2.57	54.50	1.65
8	——	——	——	7	137.0	4.90	74.7	3.86	54.58	3.59
13	150	64	57.3	29	134.1	3.84	73.2	2.09	54.59	1.47
11	144	57	60.4	5	129.4	1.80	71.5	2.98	55.26	2.27
16	——	——	——	6	134.3	5.74	74.3	4.12	55.30	0.78
10	——	——	——	8	132.6	5.29	73.4	2.98	55.34	1.74
1	161	66	56.3	23	138.9	4.37	77.1	3.30	55.54	1.62
17	——	——	——	10	137.1	3.64	76.3	3.60	55.62	1.62
3	143	58	59.4	13	136.6	3.42	76.5	1.96	55.98	1.76
6	——	——	——	17	133.7	3.54	74.9	2.75	56.05	2.32
19	140	57	59.3	17	135.1	3.66	75.9	3.06	56.16	1.38
12	——	——	——	25	133.3	4.55	75.1	2.63	56.35	1.54
7	——	——	——	6	135.8	3.62	76.5	2.38	56.56	1.66
9	——	——	——	9	134.0	3.55	75.3	2.96	56.94	1.32
15	——	——	——	5	136.8	5.02	78.0	2.56	57.02	1.20
4	——	——	——	12	135.6	3.99	77.4	4.01	57.08	2.12

H*— height, D**—depth, D%#—depth percentage, s##—standard deviation

Hook Angle

Some cattle have a tendency to toe out in the hind legs much more markedly than others, forming an angle at the hooks. This character, which in horses is called "cow-hocked," and for purposes of this study has been referred to as "hook angle," was most noticeable in a group of Ayrshires, daughters of one bull. Since no device had been perfected to measure this character, one was constructed and tested.

It was assumed that if two lines were drawn parallel to the ground and through the cleft of each hoof or parallel to the flat bone of each shank they would form an angle behind the cow corresponding to the degree of toeing out, or the hook angle. Therefore a 180 degree metal protractor with two radial hands was mounted six inches from the square end of ½ inch by 2½ inch pointed board (Fig. 7 C, Appendix). The median line 0 of the protractor was parallel to the longitudinal axis of the board and the 90 degree base lines were adjacent to the square end which formed the handle. This instrument was placed on the floor behind, or slightly between the hind legs and under the cow, with the longitudinal axis parallel and directly below the median line of the cow. The two radial hands were then set corresponding either to the flat bone of the shank of the hind leg or to an imaginary line drawn through the cleft of the hoof. For example, if the left foot toed out 15 degrees from the median line 0, and the right foot toed out 20 degrees from the median line 0, the total hook angle would be 35 degrees.

Making no attempt to keep the cows standing uniformly, a test of repeatability was designed. Four measurements were made on each of 18 Ayrshire cows during a 10 day period. By analysis of variance, in which the differences between cows was tested by the variance of measurements on the same cow, a very highly significant F value of 15.38 was obtained. This indicated a

probability of 1000 : 1 that the differences between cows were real differences and not due to the standing position of the cow or to the method of measurement. Differences between measurements never exceeded 28 degrees, the average being nearer 10 degrees. It was noticed that the variation was decreased if the cows were measured when standing with the two hind feet about eight to 12 inches apart and parallel. It was concluded that this measurement, although variable, was more objective than observational differences, especially when the positions of the cows were relatively uniform.

Since insufficient material was available on Ayrshires, it was decided to conduct this investigation on the same group of Holsteins as was used in the other study. In five different herds a total of 249 daughters of 17 different bulls were measured.

The opinion has been expressed by some breeders that the hock angle increases with age. A scatter diagram (Fig. 2) of age plotted against hock angle revealed, however, that very little if any regression or correlation existed. The true effect of age upon the hock angle could only be shown by measuring the same animals at different ages. The large number and the similarity of blood-lines of the animals in this study, however, provided a strong indication of this effect. The fact that cows less than four years old had a hock angle of more than 35 degrees (Fig. 2) was strong supporting evidence of the slight effect of age upon this character. It was noted that the combination of toeing out and sickle hocks greatly accentuated the appearance, and this may be the reason that age has been considered such an important factor.

By an analysis of variance in which a highly significant F value of 4.1 was obtained, it was determined that measurable differences existed between averages of groups of daughters of different bulls (Table 5). This,

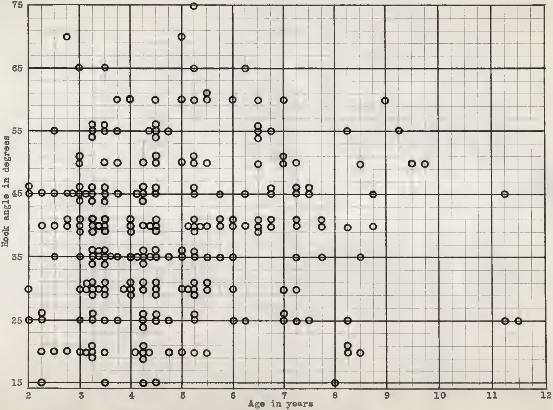


Fig. 2. Scatter diagram of hook angle plotted against age.

supporting previous observations of the character, showed that it was inherited.

The inheritance follows the pattern of an incompletely dominant character since a few cases of extreme toeing out are found in all but one group of daughters and can be assumed to be inherited from the dams. No exceptions were found among the available dam daugher comparisons. In three of the groups approximately half of the daughters toe out more than 30 degrees.

Table 6. Hock angle measurements of 249 Holstein cows grouped by sires.

Bull no.	Bull's measurement	Daughters avg.	Standard deviation	Bull no.	Bull's measurement	Daughters avg.	Standard deviation
5	25	50.4	6.55	10	—	33.6	9.16
1	25	47.6	10.20	22	—	33.5	9.57
4	—	46.7	7.16	9	—	33.3	12.50
21	33	42.1	14.10	13	28	33.1	9.20
20	35	40.6	15.30	3	—	32.1	9.06
2	25	40.0	7.56	15	—	32.0	10.95
19	26	37.4	13.74	16	—	31.7	6.05
12	—	37.0	10.77	11	30	27.5	5.78
14	—	36.2	15.64				

Out of the 17 bulls, eight were still living and were measured. No bull exceeded 35 degrees, the bull with the third greatest hock angle (30 degrees) sired the straightest legged group of daughters (27.5 degrees), and the bull with the group of daughters having the highest average (50.4 degrees) only had a hock angle of 25 degrees. Although proof is lacking this is strong evidence for the assumption that toeing out in the hind legs is a sex modified character.

Rump Slope

One of the characteristics receiving severe criticism in show ring judging of dairy cattle is sloping rump. The degree of slope from hooks to pins was accepted as the slope of the rump in this study, although it is acknowledged that the tail setting constitutes a great part of the rump slope considered in cattle judging. The angle of slope was measured with the hook angle protractor (Fig. 7C, Appendix). The longitudinal axis of the instrument was held by the pointed end parallel to the ground so that the offset handle rested on the cow's right hook bone. With the metal protractor in a vertical plane, one radial hand was pointed at the pin bone, the angle of slope being read directly in degrees. After considerable experience had been gained in measuring rump slope with this instrument it was noted that a very close estimation could be made by observation. Because the daughters of bull No. 6 were not stanchioned the instrument was not used, but a careful estimation of each animal was recorded.

Three groups of daughters were considered in this study; the 14 daughters of sire No. 21, 18 of his half sisters out of sire No. 6, and 25 daughters of sire No. 20 who was used in the same herd as the sire No. 21. The rump slope for the three bulls, and the average rump slope for the three bull's daughters are given in Table 6.

Table 6. Rump slope of 57 Holstein cows and two of their sires.

Bull no.	No. of daughters	Bull's measurement	Daughter's measurements	
21	14	10	15.8	4.9
6	18	dead	5.8	5.3
20	25	0	7.4	4.8

Fig. 3. Sire No. 21. Notice the sloping rump.

Fig. 4. Sire No. 20. Notice the level rump.

The analysis of variance gave a very highly significant F value of 13.9. It was concluded that since bull No. 21 (Fig. 3) sired rather uniformly sloping rumped daughters this condition was probably due to one or more dominant or incompletely dominant factors. This bull probably inherited most of the factors producing this condition from his dam since only three of his 18 half sisters showed the character markedly and the herdsman "remembered the dam was 'rough.'" Sire No. 20 (Fig. 4) used in the same herd produced only two out of 25 daughters equalling or exceeding the average of the daughters of sire No. 21.

Udder Characteristics

Observations were made at five different herds on the following udder characteristics: front and rear attachments, texture, and veining. For purposes of statistical analysis only 176 daughters of 11 bulls were compared in the studies of inheritance, one bull having eight daughters and all others having 10 or more.

Ratings of good, medium, or poor were given the cows on texture, veining, front attachment and rear attachment, with notations made of the light quarters. All observations were made immediately after milking and no dry cows nor recently fresh cows were included. By means of a 3 x 11 contingency table and the chi-square test (Snedecor 1940, p. 171), it was determined whether there was any significant difference between the daughters sired by one bull and those sired by any other bull.

Texture. The study of texture did not reveal a significant difference between groups of daughters of different bulls. A chi-square value of 23.4306 was obtained, which is non-significant, indicating a probability of 20 to 30 percent. It was concluded that either there were no significant difference between groups, or the errors involved in grading were so great as to mask

these differences. It was noted, however, in this study that approximately one half of the total chi-square was obtained from bull No. 3, indicating a possible exception.

Udder veining. The results obtained in the study of veining on the udder showed that this characteristic is inherited. A highly significant chi-square of 39.5838 was obtained, with a probability of less than one percent. Sires No. 6, 21, and 20 (Table 7) produced the greatest deviation from the average of the group. Bull No. 6 sired several more poorly veined daughters than the average of the entire group, while the other two bulls in a different herd, one a son of sire No. 6, sired a great number of daughters in the good class. It was concluded that the inheritance of veining must involve several genes.

Table 7. Frequency of occurrence of good, medium, and poor classes of udder veining on 176 Holstein cows.

Bull no.	No. of daughters	Good veining	Medium veining	Poor veining	Percent good
4	11	0	5	6	0.0
17	10	0	3	7	0.0
6	17	1	1	15	5.9
3	14	1	3	10	7.1
1	23	5	7	12	15.6
12	23	5	4	14	21.7
13	24	6	7	11	25.0
23	8	2	3	3	25.0
19	13	4	4	5	30.8
20	21	9	8	4	42.8
21	13	6	5	2	46.2
Total	176	37	48	91	21.02

Front and Rear Attachments. From the results obtained in the study of udder attachments it was concluded that the quality of front attachment was

probably inherited, but inheritance of rear attachment could not be demonstrated. The author found it easier to make a distinction between good, medium, and poor front attachments than between the same grades of rear attachments. It seemed probable that the error involved in assigning grades to rear udder attachments was great enough to mask any inherited differences that might exist. A significant chi-square of 31.1004 with a probability of five percent was obtained in the study of front attachment, whereas a nonsignificant chi-square of only 22.7858 with a probability of 30 percent was obtained in the study of rear attachments. Although definite proof is lacking to establish the inheritance of these characters, it has not been proved that they are not inherited.

Epilepsy in Brown Swiss

An epileptic condition observed in a purebred Brown Swiss herd has been reported by the herdsman to the Dairy Husbandry Department of Kansas State college. This condition was first noticed in a recently purchased mature bull and was characterized by the following symptoms: lowering of head, tongue showing, slight foaming around the mouth, and finally coma. At the first appearance of the symptoms a veterinarian diagnosed the case as low blood calcium and gave an injection of calcium gluconate. Since the animal recovered after this injection he was given a similar treatment in all recurring attacks. It is probable, however, that the bull would have recovered without treatment since this condition was later shown to be inherited.

Soon after the first of this bull's progeny were born, some were noted exhibiting a similar condition. None of these calves were given the calcium gluconate treatment, yet there were no fatalities. Careful records were kept in order to make a genetical analysis. There were 37 progeny of this sire born during the period November, 1940 to March, 1942. Of the 19 females nine were abnormal, and of the 18 males one died at birth and four were abnormal. The ratio of normal animals to abnormal animals, therefore, for the males was 13:4, for the females 10:9, and for both sexes as a group 23:13. The dams of the abnormal calves were out of eight different bulls and 11 different dams, the relationship between them or between them and the sire being negligible. Since the character was limited to the offspring of one sire, and since it showed in both sexes of his immediate offspring it was assumed to be an autosomal dominant factor. Only part of the offspring showed the character, indicating that the bull was heterozygous. Testing this hypothesis by the chi-square method revealed that the deviation from the expected ration of

1:1 (heterozygote bred to double recessives) was not significant. This test showed that a ratio of 23:13 would occur by chance in a 1:1 population one time out of seven.

At the present time no reliable information has been obtained concerning the immediate parents of the sire. If it could be proved that his sire or his dam had possessed the character and that one of their parents also had possessed it, the proof would be complete for its dominance.

Since through lack of penetrance of the character it may be possible for an animal to carry the factor without showing it, even though dominant, it would be inadvisable to call all normal calves of this bull non-carriers unless some further test was applied. All present evidence indicates the character to be due to single, dominant factor.

Buckled Ankles

An abnormality of the hind legs has been noted in two herds of purebred Jersey cattle. In this condition the foot is not set straight with the leg, but tends to turn in, giving a bowed appearance to the ankle (Fig. 5 and 6). This abnormality, designated as "buckled ankles," apparently is inherited as a dominant character. It is quite sharply defined in some of the older cattle, grading in expression to almost normal in some of the younger animals so that out of 29 cases studied, 11 were questionable.

Of the 29 cases, 13 could be traced to two bulls. Three more cases were found in a dam and two of her daughters by different bulls. The most striking case was shown in eight heifers from one sire, five of which were distinctly buckle-ankled, two were questionable, and one was normal. One of his two granddaughters was also affected. Observations could not be made on the sire

Fig. 5. An extreme case of buckled ankles.

Fig. 6. Same animal as Fig. 5 viewed from a different angle. Notice how the ankles bow out preventing the feet from being placed flat on the ground.

since he was no longer living, but unless the character is sex-limited he should have had buckled ankles. From the foregoing data it appears that buckled ankles is a dominant character, but varies in severity.

Wry Tail

Information on the prevalence of wry tails among Jersey cattle has been collected from six different herds in the states of Kansas, Missouri, Texas, and Colorado. Although Atkeson and Warren (1935) reported that the character seemed to occur very seldom, the data herein reported indicates that the character is rather widely disseminated throughout the Jersey breed, one herd having as many as 47 percent of the animals affected. Their conclusion that the character is inherited as a recessive, however, has been confirmed by the data presented in this study.

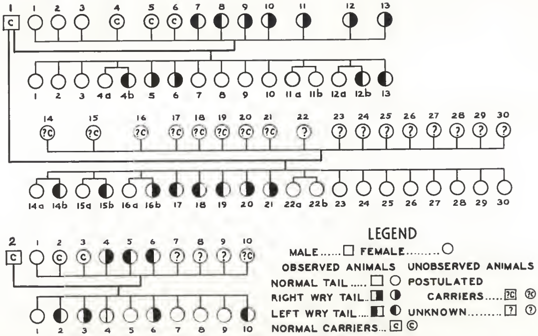
Confirmation of Recessive Mode of Inheritance. The accompanying diagrams (Plate I) show that wry tailed calves were produced when both parents appeared normal. This can only occur with a recessively inherited character. Representing wry tail by wt and normal by Wt*, both of the normal appearing bulls No. 1 and No. 2 must hve been Wtwt, or heterozygous for the character. When bull No. 1 was bred to nine wry tailed dams (Plate I) only two wry tailed offsprings were produced. According to the expected 1:1 ratio a deficiency of wry tailed offspring was produced but this was found to be non-significant by the chi-square test. Data on many more animals were recorded, but only those cases in which several daughters of one sire were observed have been used in the diagrams in Plate I to illustrate the mode of inheritance of the character. A summary of the data is given in Table 6.

*Atkeson and Warren (1935) used the symbols N and n for this character.

EXPLANATION OF PLATE I

Pedigree charts of sire No. 1 and sire No. 2 in herd No. 1 showing the occurrence of wry tail in offspring of both normal and wry tailed dams.

PLATE I

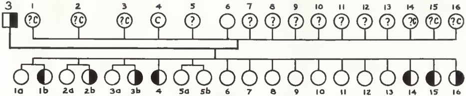


HERD I.

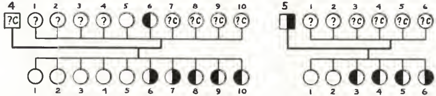
EXPLANATION OF PLATE II

Pedigree charts of sire No. 3 from herd No. 2, and sires No. 4 and No. 5 from herd No. 3 illustrating the frequency of occurrence of right and left wry tails from wry tailed and unobserved bulls.

PLATE II



HERD 2.



HERD 3.

LEGEND

MALE ..... FEMALE .....

OBSERVED ANIMALS

NORMAL TAIL ....

RIGHT WRY TAIL ....

LEFT WRY TAIL ....

NORMAL CARRIERS C

UNOBSERVED ANIMALS

POSTULATED CARRIERS .... ?C

UNKNOWN .... ?

Table 8. Summary of data collected on wry tail in Jersey cattle.

Herd	Bull no.	Progeny Normal	Progeny Wry tail Total	Progeny Wry tail WR	Progeny Wry tail WL	Dams Normal	Dams Wry tail Total	Dams Wry tail WR	Dams Wry tail WL	Unknown	Gene frequency
1	1 N	24	13	5	8	7	9	7	2	21	
	2 N	6	4	2	2	3	3	1	2	4	
	6 ?	2	6	3	3	2	2	0	2	4	
	7 ?	3	5	2	3	3	1	1	0	4	
	Others	20	19	12	7	9	6	4	2	24	
	Total	55	47	24	23	24	21	13	8	57	67.9
2	5 WR	15	7	3	4	2	0	0	0	18	
	8 ?	3	3	2	1	0	0	0	0	3	
	Others	32	3	1	2	2	0	0	0	38	
	Total	50	13	6	7	4	0	0	0	59	45.5
3	4 ?	5	5	2	3	0	1	0	1	9	
	8 WR	2	4	1	3	0	0	0	0	8	
	Others	6	4	3	1	0	2	1	1	8	
	Total	13	13	6	7	0	3	1	2	25	70.7
4	Herd	25	2	not recorded		9	0	0	0	18	27.2
5	Herd	31	12	10	2	0	not recorded			43	52.8
8	Herd	14	8	5	3	6	0	0	0	16	60.3
Grand total		188	95	51	42	43	24	14	10	218	57.9

N = normal, ? = unknown, WR = wry right, WL = wry left

Estimated wry tail gene distributions among Jersey cattle. Using this survey as representative of the herds from which the data was collected, an estimate of the gene frequency was made. The percent of the total number of chromosomes that carry the gene for a certain character is known as the gene frequency. In a recessively inherited character, the gene frequency mathematically is the square root of the proportion of times the character is observed in a population.

The theory of gene frequencies is based upon the assumption of random matings, whereas the data in Table 8 was taken from groups of segregated populations. Furthermore these herds were not representative of the same population as was indicated by the wide range of gene frequencies, 27 to 71 percent (Table 8). In spite of these limitations, the data from the six herds were added together in order to establish a general figure more of less characteristic of the entire Jersey breed. The estimated gene frequency was 57.9 percent for this entire group. Although the data assembled for this study tended to be selected from herds in which the character was pronounced, probably causing the estimated gene frequency to be larger than the true breed average, the fact remains that within the six herds studied this is a true estimation of the frequency the gene for wry tail occurs.

Bull No. 3 in herd No. 2 (Plate I) according to the calculated gene frequency of 45.4 percent for that herd, should have sired nine wry tailed and 11 normal animals among his 20 offspring. Since he was homozygous for the recessive character, wtwt, the number of his offspring that should show the character would be in direct proportion to the frequency of the occurrence of the gene, or 45.4 percent of 20. The actual proportion of offspring produced was seven wry tailed or two less than expected. Assuming bull No. 4 in herd No. 3 to be heterozygous, he should have sired 3.5 wry tailed and 6.5 normal calves out of 10, according to the estimated gene frequency of 70.7 percent for that herd. The actual number of wry tailed offspring produced, however, was five or 1.5 greater than expected. The number of wry tailed and normal offspring sired by bull No. 5 in the same herd coincided exactly with the expected number calculated from the gene frequency of 70.7 percent, four wry tailed and two normal. It has been shown by the chi-square test that the deviation in the number of wry tailed calves sired by these bulls is not

significantly different from the expected number, when the latter is calculated from the gene frequency of the individual herd, thereby confirming the mode of inheritance and the gene frequency calculations.

Another important estimation that can be made from the gene frequency is the number of carriers, or heterozygotes, not showing the character. For example, in herd No. 1 the gene frequency is 68 percent, or in terms of chromosomes, 139 of the 204 chromosomes located in the 102 head of cattle carry the gene wt. Of this 139, however, 94 are situated in the 47 animals affected, since each must genetically be homozygous wtwt. This leaves 45 wt genes to be distributed among the remaining 55 animals, only 10 therefore out of 102 being non-carriers.

Another fact demonstrating the extent to which the gene wt is probably spread throughout the Jersey breed was that in herd No. 1, made up of progeny of 27 different bulls, there were 47 wry tailed animals, which were the progeny of 16 different bulls. Since both parents must carry the factor for the recessive character before it will show in the offspring, 16 of the 27 bulls must have been carriers of the wry tail factor.

Relative occurrence and inheritance of left and right wry tails. It was mentioned in the report by Atkeson and Warren (1935), that although all cases of wry tail reported in that paper were set to the left, they were not in a position to say whether that was the more prevalent condition, or if the direction of the set was controlled by heredity. Of the 95 wry tailed animals observed in this study, 51 had their tails set to the right, 42 to the left, and two were reported as only wry tailed with no direction given (Table 8). This would justify the conclusion that the relative occurrence of wry tails set to the right or left is about equal.

Bulls No. 3 and No. 5 were both wry tailed, and both wry to the right (Plate II), but each sired both left and right wry tailed daughters. In eight dam-daughter comparisons three dams which were wry to the left produced daughters wry to the right, and all five dams which were wry to the right produced daughters wry to the left. Since the two wry tailed bulls produced both types of wry tails, and the deviation from the expected random occurrence of 1:1 was not significant, the conclusion has been reached that the direction of the set of the wry tails is not governed by heredity.

In summary, it has been shown by the foregoing data that wry tail is inherited as a recessive, and that the set of the tail either to the right or left is not governed by heredity. It has also been postulated that the gene frequency of the wry tail factor within the Jersey breed is probably between 50 and 60 percent, and that it is probably present in the other breeds but to a lesser extent.

SUMMARY AND CONCLUSIONS

1. The purpose of this study was to determine if certain body characters were inherited and, if possible, the mode of inheritance.

2. Since controlled, experimental matings were not feasible, the material for this study was collected from large numbers of animals, mostly in Kansas.

3. From head measurements made on 248 Holstein cows in one study and 69 cows of four different breeds in another study it was concluded that: (a) length and width of head are inherited independently; (b) width seems probably to be more closely associated with differences in general body size, while length is influenced by special size factors; (c) width of head varies as much between groups of daughters of one bull as it does between breeds; (d) inherited differences in length of head are due to differences in total length,

not differences in one portion of the head such as length from eye level to nose.

4. From height and body depth measurements made on 250 Holstein cows the following was concluded: (a) the condition known as legginess is an inherited character; (b) total height at withers is determined by inheritance; (c) depth of body measured just behind the shoulder points is determined by inheritance.

5. From measurements made of the hind legs of 249 Holstein cows it was concluded that: (a) although the variation within groups was great, the differences between the hock angles of groups of daughters of different bulls must be due to heredity; (b) there is strong evidence that abnormal hock angle is a sex-limited dominant character.

6. From a comparison of 57 Holstein cows and two of their sires it was concluded that slope of the rump from hip bones to pin bones was due to one or more dominant or incompletely dominant factors.

7. From observations made on the udders of 176 Holstein cows it was concluded that: (a) either there were no significant inherited differences in texture, or the errors involved in grading were too great; (b) degree of veining on the udder was inherited, probably due to several genes; (c) strength of front attachment was probably determined by inheritance; (d) the grades of rear attachment were not sharply enough defined to determine any significant differences.

8. An epileptic character in Brown Swiss was found to be due to a single, dominant factor.

9. An abnormality of the hind legs in Jerseys designated in this paper as buckled ankles appeared to be a dominant factor although varying in severity.

10. From observations made on 216 Jersey cattle in four states it was concluded that: (a) wry tail in Jersey cattle is inherited as a single recessive; (b) the direction of the set of the tail is not governed by heredity; (c) the recessive gene producing wry tail was estimated to be present in 58 percent of the cattle studied, and this estimation was offered as being more or less characteristic of the Jersey breed.

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APPENDIX

EXPLANATION OF PLATE III

Fig. 1. Average depth percentage of groups of daughters arrayed according to sires beginning with the most "leggy" group.

Fig. 2. Average length of head in centimeters of groups of daughters arrayed according to sires.

Fig. 3. Average height in centimeters of groups of daughters arrayed according to sires.

Fig. 4. Average hook angle in degrees of groups of daughters arrayed according to sires.

PLATE III

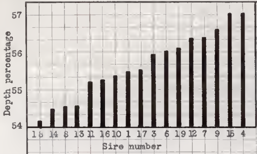

Fig. 1

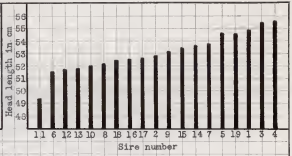

Fig. 2.

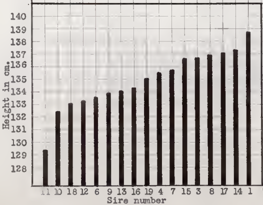

Fig. 3

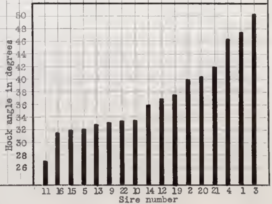

Fig. 4

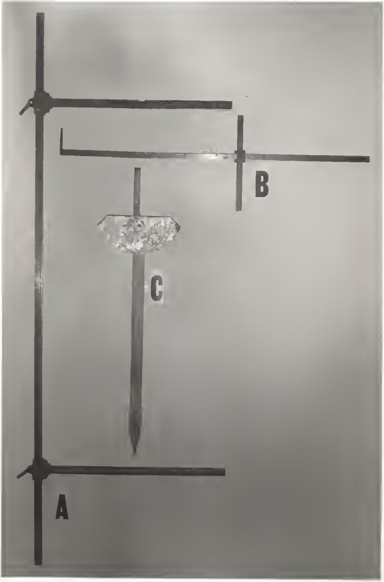

Fig. 7. Instruments for measuring: A--body depth, B--head, and C--hook angle and rump slope.

Table 9. Suggested list of some heritable body characters in dairy cattle.[1]

Character	Breeds possessing the character
Hind legs	
Cow-hocked	Holstein, Ayrshire, Guernsey, Jersey
Sickle-hocked	Holstein, Ayrshire, Guernsey, Jersey
Post or hog-legged	Brown Swiss, Holstein, Jersey, Ayrshire
Weak pasterns	Guernsey
Buckled ankles	Jersey (Guernsey)
Crampy or rheumatic	Holstein, Ayrshire
Fore legs	
Toeing out	All breeds
Head	
Dished face	Jersey
Twisted face	Jersey
Roman nose	Holstein
Non-typical high horns	Jersey, Guernsey
Loose horns	Jersey, Holstein, (Guernsey)
Undershot jaw	Jersey
Parrot jaw	Jersey
Fuzzy ears	Brown Swiss
Lop ears	Brown Swiss
Miscellaneous	
Wing shoulders	Guernsey
Short last rib	Jersey
Cryptorchid	Jersey, Holstein, Guernsey
Nervousness	Jersey, Holstein, Ayrshire

[1]Suggested by Prof. F. W. Atkeson.

Table 10[1]. Color genes in cattle and a brief summary of their effects.[2]

Dominant gene	Color of animal	Recessive gene	Color of animal
C	Pigment	c	Albino (no pigment)
B	Black hair, black pigment in skin, hoof tongue, etc., in absence of white-spotting genes.	b	Usually red
Bs	Black spotting, as in Jerseys and Ayrshires. There are multiple-factor modifiers of black spotting. Much black dominant in males and little black dominant in females.	bs	No black spotting.
Br	Brindle - causes black (Bs) to form in stripes on a background of red. No effect in animal with the gene B, which is epistatic, that is, covers up the brindle characteristic.	br	Not brindle.
D	Dilutes black to dun and red to yellow color.	d	No dilution.
I	No dilution .	i	Dilutes black to dun and red to yellow color.
N	Hair of any color becomes devoid of color or white. Heterozygote, Nn, is a roan.	n	Some pigment.
Rn	No effect on color.	rn	Changes roan to red.
Wn	Pigmented hair	wn	White (Affects hair but not skin. Silver gray of Nellores cattle of Philippines).
W	Lack of whitening.	w	Whitening, causing white muzzle and whitish hairs in ears, on the belly, udder, and inside of rear legs; sometimes extends over whole body.
Ps	Black-pigmented skin spots (most easily seen on nose or udder). May occur anywhere on body.	ps	Absence of black skin spotting.
Wp	White spotting. Found in English white park cattle.	wp	Lack of dominant white
In	White spotting in the inguinal region	in	Absence of white spotting in the inguinal region.

Table 10. (Contd.)

Dominant gene	Color of animal	Recessive gene	Color of animal
	Spotting Series of Multiple Allelomorphs		
Sh	Hereford whiteface pattern		See S and s
S	Self-colored (entirely pigmented	s	White spotting in coat and unpigmented areas.
SD_1	Dutch Belted pattern. Allelomorphic to and dominant over S and s		See S and s
SC	Causes dominant white-spotting color-sided pattern. Allelomorphic to S and s, incompletely dominant to S, completely dominant to s.		Do.
	Modifiers of Spotting Series		
Rn	Red-neck - modifier of SH (and s), causing dorsal portion of neck and shoulders to be red.	rn	Absence of red-neck color.
Re	Modifier of SH, causing red hair around each eye.	re	Absence of red hair around eyes.
Lw	Modifies white spotting to produce little white in coat, tongue, nose, etc.	lw	Increased amount of white.
Pl	Modifies s to produce little or no white below the knees. Pigment starts at hoofs and works upward.	pl	Almost entirely white below knees.

[1] Black, W. H. Beef and dual purpose cattle breeding. Yearbook of agriculture. U. S. Dept. of Agr., Washington, D. C. p. 865-886. 1936.

[2] Mostly from Ibsen, H. L. Cattle inheritance. I. Color. Genetics 18:441-480. 1933.

Table 11. Miscellaneous inherited characters of cattle.

Character	Mode of inheritance	Reported by	Date	Publication
Zebu skeleton dewlap ear musculature	Appeared to be dominant to Italian cattle	Carlo Pucci	1910	Jour. Hered. 6(3):144.
Beef quality in fore quarters, Dairy quality in rear quarters	Appears to be dominant	J. W. Gowen	1918	Jour. Agr. Res. 16(1):1-58.
High milk yield Low fat percentage	Appeared to be dominant	J. W. Gowen	1920	Jour. Agr. Res. 11(7): 300-316.
Polydactylism	Dominant	Elmer Roberts	1921	Jour. Hered. 12(2):84-86.
Notched ear	Variable dominant	Jay L. Lush	1922	Jour. Hered. 13(1):8-13.
Double ear	Dominant	Jay L. Lush	1924	Jour. Hered. 15(2):93-96.
Polled	Dominant	Reviewed by R.C.M. Auld	1927	Jour. Hered. 18(7):309-321.
Duck-legged	Dominant	Jay L. Lush	1930	Jour. Hered. 21(2):84-90.
Hernia	Apparently a sex-limited dominant	T. R. Warren and F. W. Atkeson	1931	Jour. Hered. 22(11):345-352.

Table 11. (Contd.)

Zebu horn size	Appeared to be recessive to Italian cattle	Carlo	1910	Jour. Hered. 6(3):144.
Congenital cataract	Recessive	J. A. Detlefsen and W. W. Yapp	1920	Amer. Nat. 54(632):277-280.
One teat only on one side of udder	Recessive	Edwin E. Heizer	1932	Jour. Hered. 23(3):111-114.
Semi-hairlessness	Recessive	W. A. Craft and W. L. Blizzard	1934	Jour. Hered. 25(10):384-390.
Wry tail	Recessive	F. W. Atkeson and T. R. Warren	1935	Jour. Hered. 26(8):331-334.
Screw tail	Recessive modified	Bradford Knapp, Jr. M. W. Emmel and W. F. Ward	1936	Jour. Hered. 27(7):269-271.
Defective hair and teeth	Not known	L. J. Cole	1919	Jour. Hered. 10(7):303-306.
Twinning	Not determined	Robert H. Lush	1925	Jour. Hered. 16(8):273-279.
Double muscled	Not known	Reported as early as 1886. Also by A. D. Weber and Herman L. Ibsen	1934	Amer. Soc. Anim. Prod. Proc. 1934:228-232.

Table 12. Inherited lethal characters in dairy cattle.*

Character	Mode of inheritance	Reported by	Date	Publication
Achondroplasia$_1$	Dominant	J. Wilson	1908	Proc. Roy. Dublin Soc. N. S. 12:1-17.
Congenital ichthyosis	Recessive	E. Lesser	1914	Lehrb. der Haut-u. Geschlecht-Krankh. 13 aufl. Berlin.
Congenital epithelial defect (epitheliogenesis imperfecta)	Recessive	L. J. Cole	1919	Jour. Hered. 18(11):487-495.
Achondroplasia$_2$	Recessive	O. L. Mohr and Chr. Wriedt	1925	Zeitschr. f. Tierz. u. Zuchtungsbiol 3:223-230.
Foetal resorption	Not known	C. W. Turner	1927	N. Amer. Vet. 8(11):27-31.
Hairless (hypotrichosis congenita)	Recessive	O. L. Mohr and Chr. Wriedt	1927	Jour. Genet. 19:315-336.
Amputated legs	Recessive	O. L. Mohr and Chr. Wriedt	1928	Jour. Genet. 20:187-215.
Muscle contracture	Recessive	O. L. Mohr	1930	Jour. Hered. 26(1):46.
Ossification of articulation of lower jaw	Recessive	O. L. Mohr	1930	Naturens Verden 14:1-31.
Hind legs lame	Probably recessive	K. Loje	1930	Tidskrift. f. Landokonomi 10:517-549.

Table 12. (Contd.)

Mumification	Recessive	K. Loje	1930	Tidskrift. f. Landokonomi 10:517-549.
Short spine	Recessive	O. L. Mohr and Chr. Wriedt	1930	Jour. Genet. 22:279-297.
Short limbs	Recessive	K. Ljutikow	1932	Jour. Biol. 1:21-51.
Hairlessness	Recessive	W. M. Regan, S. W. Mead, and P. W. Gregory	1935	Jour. Hered. 26(9):355-368.
Congenital dropsy	Probably single recessive	E. L. Larsson	1935	Lantbr. Veck. Handl. p. 310-331.
Ossification of all joints	Probably recessive	W. Schaper	1936	Zeitsch. f. Zuchtung B. 35:1-88.
Impacted molars	Probably recessive	E. E. Heizer and M. C. Hervey	1937	Jour. Hered. 28(2):123-128.
Skull defect	Unknown	A. O. Shaw	1938	Jour. Hered. 29(8):319-320.
Agnathia	Recessive	Fordyce Ely, F. E. Hull and H. B. Morrison	1939	Jour. Hered. 30(3):105-108.

* All but the last two characters taken from Eaton, O. N. A summary of lethal characters in animals and man. Jour. Hered. 28(9):320-326. 1937.